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Conioscypha tenebrosa sp. nov. (Conioscyphaceae) from China and notes on *Conioscypha* species

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Abstract

Conioscypha is an asexual morph genus placed in the family Conioscyphaceae. During our study of brown-spored hyphomycetes, a new taxon *C. tenebrosa* was found on decaying wood collected in Guizhou Province, China. The new species is characterized by having micronematous, hyaline conidiophores which are often reduced to conidiogenous cells, with a cup-shaped, percurrently developed, multi-collaretted phialide, and globose to subglobose, obovoid conidia with broadly rounded apex and subtruncate base. The phylogenetic analysis of combined LSU, SSU, ITS and *RPB2* sequence data showed that isolates of *C. tenebrosa* are phylogenetically distinct from other species. *Conioscypha tenebrosa* sp. nov. is therefore introduced here with a description and morphological illustration. Taxonomic notes and a morphological comparison of *Conioscypha* species are provided.

Keywords: 1 new taxon, asexual fungi, multi-gene phylogeny, Sordariomycetes, taxonomy

Introduction

The genus *Conioscypha* was introduced by von Höhnel (1904) with *C. lignicola* Höhn. as the type species. Shearer (1973) revised the description of *C. lignicola* and introduced the second species *C. varia* Shearer with morphologically variable conidia. She pointed out that cup-like, one to several collaretted phialide, formed by layers of ruptured walls in the process of conidial production is characteristic of the genus (Shearer 1973). Subsequently, several *Conioscypha* species were introduced worldwide. In this study, we accept 17 species in *Conioscypha* of which *C. aquatica* Z.L. Luo, K.D. Hyde & H.Y. Su, *C. submersa* Z.L. Luo, K.D. Hyde & H.Y. Su and *C. taiwaniana* J.L. Chen and S.S. Tzean were initially described from China (Chen & Tzean 2000, Luo *et al.* 2019).

Réblová & Seifert (2004) described the ascomycetous genus *Conioscyphascus* Réblová & Seifert based on *Co. varius* Réblová & Seifert, characterized by inconspicuous, superficial or immersed, ostiolate, subhyaline to pale orange ascomata with hyaline, 8-spored, unitunicate asci with a refractive J- apical annulus, and fusiform 3–7-septate ascospores (Réblová & Seifert 2004). *Conioscyphascus varius* was observed to produce *Conioscypha varia* asexual morphs in culture. The connection between *Conioscypha* and *Conioscyphascus* was also confirmed by phylogenetic analyses of LSU sequence data (Réblová & Seifert 2004). Due to nomenclatural priority (Turland *et al.* 2018), *Conioscyphascus* was synonymized under *Conioscypha*. Zelski *et al.* (2015) reported the second sexual morph of *Conioscypha*, *C. peruviana* Zelski, Raja, A.N. Mill & Shearer, which also produces asexual morph in culture.

Five *Conioscypha* species, namely *C. japonica* Udagawa & Toyaz., *C. lignicola*, *C. minutispora* Hern.-Restr., Gené & Guarro, *C. peruviana* and *C. varia* formed a distinct monophyletic clade closely related to the orders Pleurotheciales (Réblová *et al.* 2016) and Savoryellales (Boonyuen *et al.* 2011) in the phylogenetic analyses of combined LSU, SSU and *RPB2* sequence data performed by Réblová *et al.* (2016) who, therefore, established the monotypic order Conioscyphales and family Conioscyphaceae in the subclass Hypocreomycetidae (Sordariomycetes). However, Hongsanan *et al.* (2017) placed Conioscyphales in Savoryellomycetidae in their updated phylogeny of Sordariomycetes, and this was followed in the outline of Ascomycetes 2017 (Wijayawardene *et al.* 2017, 2018).

During our study on dematiaceous hyphomycetes, two interesting *Conioscypha* collections were encountered from different locations in China. Detailed morphological study and molecular analysis of combined LSU, SSU, ITS and *RPB2* sequence data indicated that these two isolates represent a phylogenetically distinct lineage and clustered together with other *Conioscypha* species. Therefore, we introduced *C. tenebrosa* *sp. nov.* and provide a morphological comparison and notes on *Conioscypha* species.

Materials & Methods

Collections and examination of specimens

Fresh samples of decaying wood were collected from Guizhou Province in southwestern China. The samples were processed and examined following the method described by Luo *et al.* (2018). The samples were incubated in plastic boxes with sterile and moist tissue at 25–30 °C for 3 days, and then examined using a stereo microscope (SteREO Discovery v8, Göttingen, Germany) attached with Axio Cam ERc5s (Göttingen, Germany). Fruiting bodies of the new taxon were mounted in a drop of water for microscopic studies and photomicrography. The species were examined with a Nikon ECLIPSE 80i (Tokyo, Japan) compound microscope fitted with a Cannon 70D (Tokyo, Japan) digital camera. Measurements were performed using the Tarosoft (R) Image Frame Work software (Liu *et al.* 2010) and photo-plates were prepared using Adobe Photoshop CS3 software (Adobe Systems, USA).

Single spore isolations were carried out following the method described in Chomnunti *et al.* (2014). Germinated conidia were individually transferred to potato dextrose agar (PDA) (Santa Maria, USA) media plates and incubated at 25 °C. Dried specimens were deposited in the herbarium of Mae Fah Luang University (MFLU), Chiang Rai, Thailand. Pure cultures were deposited in the Guizhou Culture Collection (GZCC), Guiyang, China. Facesoffungi (FOF) numbers were acquired as in Jayasiri *et al.* (2015) and Index Fungorum numbers as in Index Fungorum (2019)

DNA extraction, PCR amplification and sequencing

A sterile scalpel was used to scrape fresh mycelia from pure cultures growing on PDA medium for one month at 25 °C. Genomic DNA was extracted using DNA Extraction Kit (Sangon Biotech, Shanghai, P.R. China) following the manufacturer's protocol. Four different gene regions, the nuclear large subunit rDNA (28S, LSU), the nuclear small subunit rDNA (18S, SSU), internal transcribed spacer (ITS) and the RNA polymerase second largest subunit (*RPB2*) were selected for study, because these gene regions are suitable to study Sordariomycetes (Tang *et al.* 2007). Part of LSU locus was amplified with the primers LR0R and LR5 (Vilgalys & Hester 1990), part of SSU with primers NS1 and NS4 (White *et al.* 1990), part of ITS with primers ITS5 and ITS4 (White *et al.* 1990) and part of *RPB2* with primers fRPB2-5F and fRPB2-7cR (Liu *et al.* 1999). Polymerase chain reaction (PCR) was carried out in 25 µl reaction volume containing 12.5 µl 2 × PCR Master Mix (TIANGEN Co., P.R. China), 9.5 µl ddH₂O, 1 µl of each primer and 1 µl DNA template. The PCR thermal cycle program for LSU, SSU and ITS were as follows: 3 min at 94 °C (initial denaturation), followed by 40 cycles of 45 s at 94 °C (denaturation), 50 s at 56 °C (annealing), 1 min at 72 °C (extension), with a final extension of 10 min at 72 °C. The PCR thermal cycle program for *RPB2* was as follows: 5 min at 95 °C (initial denaturation), followed by 40 cycle of 1 min at 95 °C (denaturation), 2 min at 52 °C (annealing), 90 s at 72 °C (extension), with a final extension of 10 min at 72 °C. The PCR products were examined using 1% agarose electrophoresis gel stained with ethidium bromide. Purified PCR products were sequenced by Sangon Biotech (Shanghai, P.R. China).

Phylogenetic analysis

The related sequences (**TABLE 1**) used for this study were obtained from GenBank according to the results of blast searches and other published researches (Réblová & Seifert 2004, Zelski *et al.* 2015, Réblová *et al.* 2016, Chuaseeharonnachai *et al.* 2017, Crous *et al.* 2018; Luo *et al.* 2019). Partial nucleotide sequences of the LSU, SSU, ITS and *RPB2* ribosomal RNA were used to determine the phylogenetic position of the new taxon. The multiple alignments were automatically performed using BioEdit (Hall 1999). Four genes were combined using the same software. Alignments were checked visually and optimized manually using AliView (Larsson 2014) where necessary. The final alignment was deposited in TreeBASE (submission ID: 24629). Sequences derived in this study were deposited in GenBank (**TABLE 1**).

TABLE 1. Taxa used in this study.

Species	Strain	LSU	ITS	SSU	<i>RPB2</i>
<i>Adelosphaeria catenata</i>	CBS 138679*	NG_057081	NR_145396	NG_061211	KT278743
<i>Ascotaiwania fusiformis</i>	MFLUCC 15–0621*	KX550893	MG388215		KX576871
<i>Ascotaiwania mitriformis</i>	HKUCC 3706	AF132324			
<i>Ascotaiwania sawadae</i>	SS 00051	HQ446363	HQ446340	HQ446283	HQ446418
<i>Brachysporiella setosa</i>	HKUCC 3713	AF132334			
<i>Canalisporium exiguum</i>	SS 00809	GQ390281	GQ390296	GQ390266	
<i>Canalisporium grenadoideum</i>	BCC 20507*	GQ390267	NR_111442		
<i>Canalisporium pulchrum</i>	SS 03982	GQ390277	GQ390292	GQ390262	
<i>Conioscypha aquatica</i>	MFLUCC 18–1333*	MK835857	MK878383		
<i>Conioscypha bambusicola</i>	JCM 7245	NG_059037	NR_154660		
<i>Conioscypha boutwelliae</i>	CBS 144928*	LR025183	LR025182		
<i>Conioscypha hoehnelii</i>	FMR 11592	KY853497	KY853437	HF937348	
<i>Conioscypha japonica</i>	CBS 387.84	AY484514		JQ437438	JQ429259
<i>Conioscypha lignicola</i>	CBS 335.93	AY484513		JQ437439	JQ429260
<i>Conioscypha minutispora</i>	FMR 11245*	KF924559	NR_137847	HF937347	
<i>Conioscypha nakagirii</i>	BCC77658*	KU509985	KY859266	KU509984	KU513952
<i>Conioscypha nakagirii</i>	BCC77659	KU509987	KY859267	KU509986	KU513953
<i>Conioscypha peruviana</i>	CBS 137657*	NG_058867			
<i>Conioscypha pleiomorpha</i>	FMR 13134*	KY853498	KY853438		
<i>Conioscypha submersa</i>	MFLU 18–1639*	MK835856	MK878382		
<i>Conioscypha tenebrosa</i>	GZCC 19–0217*	MK804508	MK804506	MK804510	MK828514
<i>Conioscypha tenebrosa</i>	GZCC 19–0218	MK804509	MK804507	MK804511	MK828515
<i>Conioscypha varia</i>	CBS 602.70	MH871654	MH859868		
<i>Conioscypha varia</i>	CBS 436.70	MH871548	MH859785		
<i>Conioscypha varia</i>	CBS 604.70	MH871656	MH859869		
<i>Conioscypha varia</i>	CBS 603.70	MH871655			
<i>Helicoascotaiwania hughesii</i>	DAOM 241947	JQ429230	JQ429145		
<i>Melanotriconum ovale</i>	CBS 138743*	KT278709	KT278724	KT278696	KT278745
<i>Phaeoisaria fasciculata</i>	CBS 127885*	KT278705	KT278719	NG_063057	KT278741
<i>Phaeoisaria microspora</i>	MFLUCC 16–0033*	MF167351	MF671987		MF167352
<i>Phaeoisaria sedimenticola</i>	CGMCC 3.14949*	JQ031561	JQ074237		
<i>Phragmocephala stemphylioides</i>	DAOM 673211	KT278717	KT278730		
<i>Plagiascoma frondosum</i>	CBS 139031*	KT278713		NG_061212	KT278749
<i>Pleurotheciella centenaria</i>	DAOM 229631*	JQ429234	JQ429151	JQ429246	JQ429265
<i>Pleurotheciella rivularia</i>	CBS 125238*	JQ429232	JQ429160	NG_061124	JQ429263
<i>Pleurotheciella uniseptata</i>	DAOM 673210*	KT278716	KT278729		
<i>Pleurothecium floriforme</i>	MFLUCC 15–0628*	KY697277	KY697281	NG_063634	
<i>Pleurothecium recurvatum</i>	CBS 138747	KT278714	KT278728	KT278703	
<i>Pleurothecium semifecundum</i>	CBS 131271*	JQ429240	JQ429159	NG_062854	JQ429270
<i>Savoryella longispora</i>	SAT 00322	HQ446380	HQ446359	HQ446302	HQ446450
<i>Savoryella paucispora</i>	SAT 00866	HQ446381	HQ446360	HQ446303	HQ446451
<i>Savoryella verrucosa</i>	SS 00052	HQ446374	HQ446353	HQ446296	HQ446445
<i>Sterigmatobotrys macrocarpa</i>	DAOM 230059	GU017316			
<i>Sterigmatobotrys macrocarpa</i>	PRM 915682	GU017317	JQ429153	JQ429255	
<i>Sterigmatobotrys rudis</i>	DAOM 229838	JQ429241	JQ429152	JQ429256	JQ429272

*The newly obtained strains are indicated in bold. Ex-type strains are indicated with * after collection number.

Maximum likelihood analysis was performed using RAxML (Stamatakis 2006). The tree search included 1,000 non-parametric bootstrap replicates and the best scoring tree was selected from suboptimal trees under the GTRGAMMA substitution model. The resulting replicates were plotted on to the best scoring tree obtained previously.

Maximum parsimony analysis was performed with the heuristic search in PAUP v. 4.0b10 (Swofford 2002). Gaps in the alignment were treated as missing characters and all characters were unordered. Maxtrees were unlimited. Branches of zero length were collapsed and all multiple, equally parsimonious trees were saved. Clade stability was assessed using a bootstrap (BT) analysis with 1,000 replicates, each with 10 replicates of random stepwise addition of taxa (Hillis & Bull 1993).

Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.* 2012). The program MrModeltest 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model for each data partition. GTR+I+G substitution model with gamma rates and dirichlet base frequencies was decided for LSU, SSU, ITS and *RPB2* sequences. The Markov Chain Monte Carlo (MCMC) sampling approach was used to calculate posterior probabilities (PP) (Rannala & Yang 1996). Bayesian analyses of four simultaneous Markov chains were run for 1,000,000 generations with trees sampled every 1,000th generations. The first 20% of trees, representing the burn-in phase of the analyses, were discarded and the remaining trees were used for calculating posterior probabilities (PP) in the majority rule consensus tree.

Trees were visualized with FigTree v1.4.0 (Rambaut 2006) and the layout was edited using Adobe Illustrator CS6 software (Adobe Systems, USA).

Abbreviation: **BCC:** BIOTEC Culture Collection, Thailand; **CBS:** CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; **CGMCC:** China General Microbiological Culture Collection Center, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China; **DAOM:** Canadian Collection of Fungal Cultures, Agriculture and Agri-Food Canada, Ottawa, Canada; **FMR:** Facultat de Medicina i Ciències de la Salut, Reus, Spain; **GZCC:** Guizhou Culture Collection, Guiyang, China; **HKUCC:** The University of Hong Kong Culture Collection, Hong Kong, China; **JCM:** Japan Collection of Microorganism, RIKEN BioResource Center, Japan; **MFLU:** the herbarium of Mae Fah Luang University, Chiang Rai, Thailand; **MFLUCC:** Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; **PRM:** Mycological Herbarium in the National Museum in Prague, Czech Republic; Isolates with the prefix **SS** and **SAT** are from the BIOTEC Culture Collection (BCC)

Results

Phylogenetic analyses

Partial nucleotide sequences of the LSU, SSU, ITS and *RPB2* ribosomal RNA were used to determine the phylogenetic position of the new taxa. 43 strains retrieved from GenBank representing Conioscyphaceae (Conioscyphales), Pleurotheciaceae (Pleurotheciales) and Savoryellaceae (Savoryellales), along with the outgroup *Plagiascoma frondosum* CBS 139031 in Fuscosporellaceae (Fuscosporellales) were analysed. Single gene analyses were carried out to compare the topologies and clade stabilities, respectively. The manually adjusted LSU, SSU, ITS and *RPB2* alignment comprised a total of 4298 characters (1,212 for LSU, 1,236 for SSU, 705 for ITS, 1,145 for *RPB2*), including coded alignment gaps. Among them, 2,582 characters were constant, 454 variable characters were parsimony-uninformative, and number of parsimony-informative characters was 1,262. Fifteen equally most parsimonious trees (Tree length = 5645, CI = 0.497, RI = 0.650, RC = 0.323, HI = 0.503) were yielded from the heuristic search. Maximum parsimony, maximum likelihood and Bayesian analyses of the combined dataset inferred similar topologies, respectively.

The most likely tree (-ln = 30777.970605) is presented (**FIGURE 1**). The matrix had 1,975 distinct alignment patterns with 42.56% of undetermined characters or gaps. The two new *Conioscypha* strains representing one species clustered together with maximal support (ML-bs = 100%, MP-bs = 100%, PP = 1.00). *Conioscypha tenebrosa* formed a sister clade with two recently introduced species, *C. aquatica* and *C. submersa*, but the monophyly of these three species was not well-supported. Two *C. nakagirii* strains formed a basal clade in the Conioscyphaceae clade. In addition, the Pleurotheciaceae clade was sister to Savoryellaceae clade, and the monophyly of these two clades was strongly supported by ML and Bayesian analyses.

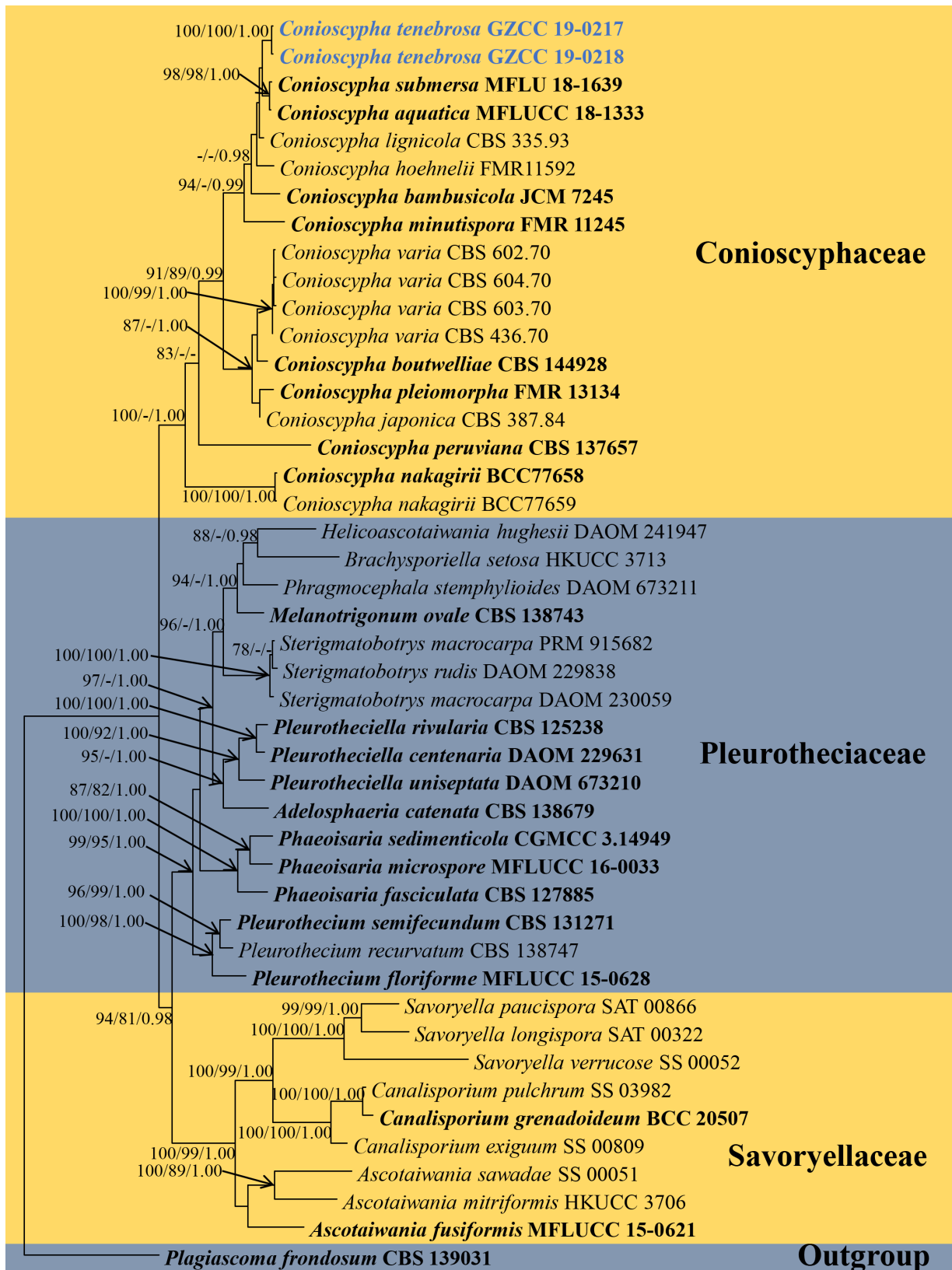


FIGURE 1. Maximum likelihood (RAxML) tree based on analysis of a combined dataset of LSU, SSU, ITS and *RPB2* sequence data. Bootstrap support values for ML and MP greater than 75% and Bayesian posterior probabilities greater than 0.95 are given near nodes, respectively. The tree is rooted with *Plagiascoma frondosum* (CBS 139031). The ex-type strains are indicated in bold and the new isolates are in bold and blue.

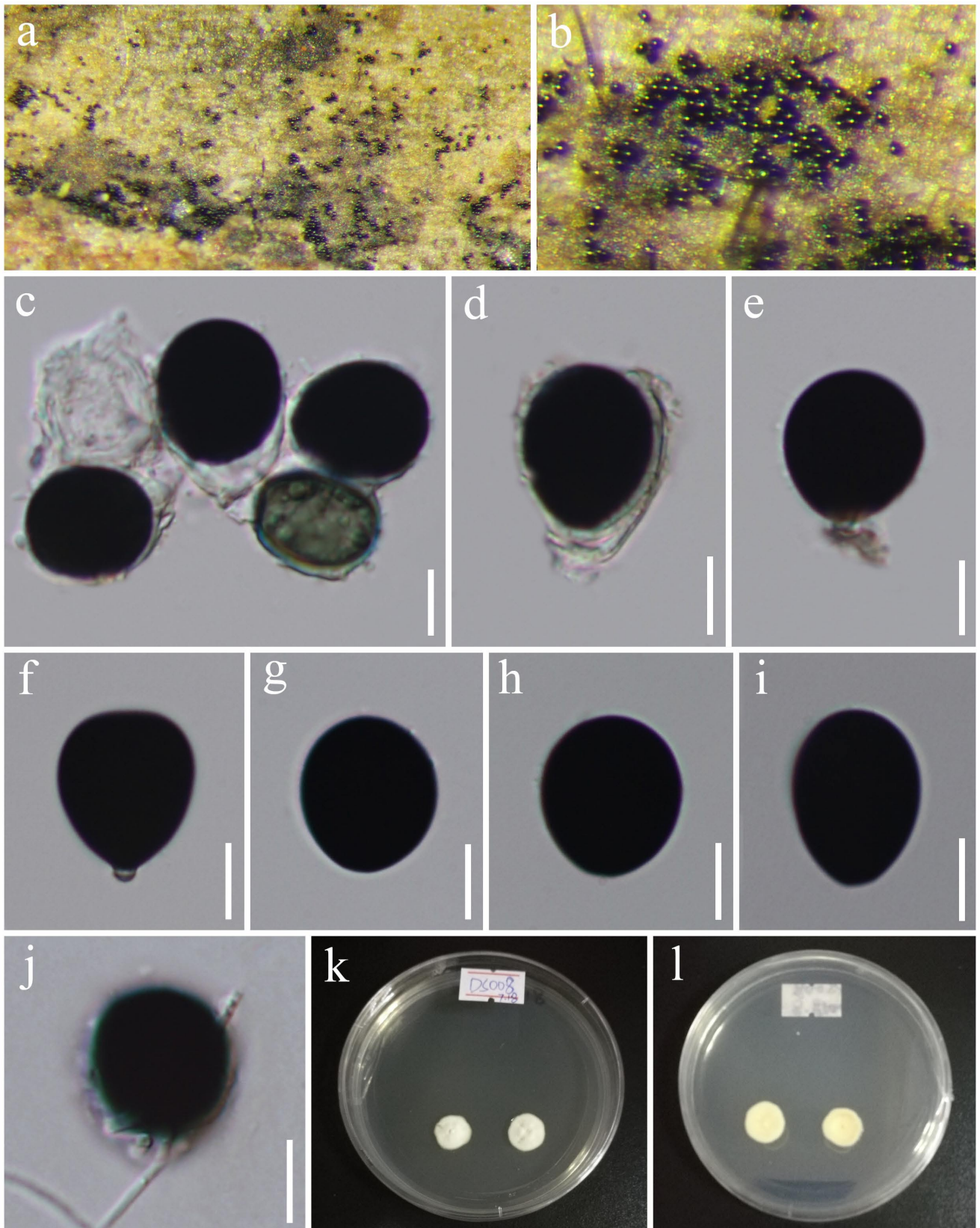


FIGURE 2. *Coniosecypha tenebrosa* (MFLU 19-0688, holotype) **a, b** Colonies on natural substrate. **c, d** Conidia and conidiogenous cells with cup-shaped multi-collarette. **e** Conidium and conidiogenous cell initiated from a hypha. **f–i** Conidia. **j** Germinated conidium. **k, l** Colonies on PDA. Scale bars: **c–j** = 10 μ m.

Taxonomy

Conioscypha tenebrosa N.G. Liu, K.D. Hyde & J.K. Liu, *sp. nov.*

Index Fungorum: IF556461; Facesoffungi number: FoF 06118

Etymology: Named after its dark conidia

Holotype: MFLU 19–0688

Saprobic on decaying wood in terrestrial habitat. **Sexual morph:** Undetermined. **Asexual morph:** Hyphomycetous. *Colonies* on natural substrate effuse, solitary, black. *Mycelium* immersed, composed of hyaline, septate, branched, smooth hyphae. *Conidiophores* micronematous, mononematous, arising directly from the hyphae, hyaline, often reduced to conidiogenous cells. *Conidiogenous cells* phialidic, integrated, sessile or on short conidiophores, hyaline, subcylindrical, smooth-walled, percurrently proliferating, with cup-shaped multi-collarete. *Conidia* formed singly, globose to subglobose, obovoid, olivaceous when young, dark brown to black when mature, smooth-walled, aseptate, broadly rounded at apex, subtruncate at base, 18–25 × 14–20 µm (\bar{x} = 21 × 17 µm, n = 30). Conidia formed by percurrent regeneration of the apex of the conidiogenous cell at same level.

Culture characteristics: Conidium germinated on water agar within 12 hours. Germ tubes produced circumferentially. Colonies on PDA media grow slowly. Mycelia superficial, circular, dense, white from above, yellowish white from below.

Material examined: CHINA, Guizhou Province, Dushan (25°58.13'N, 107°33.59'E), on decaying wood in a bank of a small freshwater, 6 July 2018, N.G. Liu, DS008 (MFLU 19–0688, holotype; ex-type living culture, GZCC 19–0217); CHINA, Guizhou Province, Zunyi, Wangcao (28°12.30'N, 107°10.24'E), on decaying wood, 15 September 2018, N.G. Liu, KKS021 (MFLU 19–0687, GZCC 19–0218)

Notes: *Conioscypha tenebrosa* resembles *C. aquatica*, *C. hoehnelii* and *C. submersa* in having subglobose conidia. However, the conidia of *C. hoehnelii* are sometimes irregular and often have a central pore in the inconspicuous scar at the base, which is absent in *C. tenebrosa*. Although, *Conioscypha tenebrosa* shares similar conidial size to *C. aquatica* and *C. submersa* (18–25 × 14–20 µm, 19–23 × 17–21 µm and 17–19 × 15–17 µm, respectively), phylogenetic analyses indicated that they are phylogenetic distinct species (**FIGURE 1**). Comparisons of ITS sequences showed that there are 22 bp (base pair) differences without gaps between *C. tenebrosa* and *C. aquatica*, and 23 bp differences without gaps between *C. tenebrosa* and *C. submersa*.

Notes on accepted *Conioscypha* species

1. *Conioscypha aquatica* Z.L. Luo, K.D. Hyde & H.Y. Su, Fungal Diversity (2019)

Description and illustration: see Luo *et al.* (2019)

Notes: Luo *et al.* (2019) introduced *C. aquatica* from freshwater habitat in Yunnan Province, China. See notes on *C. tenebrosa*. Type material of this species is MFLU 18–1640.

2. *Conioscypha bambusicola* Matsush., Icones Microfungorum a Matsushima lectorum: 38 (1975)

Description and illustration: see Matsushima (1975) and Chen & Tzean (2000)

Notes: *Conioscypha bambusicola* was introduced by Matsushima (1975) who collected this species from *Phyllostachydis edulis* (Carrière) J.Houz. in Kyoto, Japan. Subsequently, he found this fungus from bamboo in Iriomote Island, Okinawa Prefecture, Japan. This species has also been reported in *Phyllostachys* sp. from Taiwan, China (Chen & Tzean 2000). *Conioscypha bambusicola* differs from other *Conioscypha* species in having conidia with apiculate apex. Type material of this species is MFC-1891.

3. *Conioscypha boutwelliae* Hern.-Rest., Persoonia 41: 345 (2018)

Description and illustration: see Crous *et al.* (2018)

Notes: *Conioscypha boutwelliae* was introduced by Crous *et al.* (2018). The fungus was isolated from soil in the Netherlands. Conidia of *C. boutwelliae* and *C. lignicola* both have dark dots deposited at the periphery. See notes on *C. lignicola*. Type material of this species is CBS H-23743.

4. *Conioscypha dimorpha* Matsush., Matsushima Mycological Memoirs 9: 7 (1996)

Description and illustration: see Matsushima (1996)

Notes: Matsushima (1996) described *Conioscypha dimorpha* from decayed leaves in Hogsback Forest Reserve, South Africa. *Conioscypha dimorpha* is the only species in *Conioscypha* that can form both macroconidia and microconidia. Type material of this species is MFC-5A084.

5. *Conioscypha fabiformis* Matsush., Matsushima Mycological Memoirs 7: 47 (1993)

Description and illustration: see Matsushima (1993)

Notes: *Conioscypha fabiformis* has been reported from decayed leaves and wood in Loreto, Peru and decaying petioles of palm in Oriente, Ecuador by Matsushima (1993). The conidia of *C. fabiformis* is similar to the macroconidia of *C. dimorpha*, which both are oblong. However, conidia of *C. fabiformis* are slightly curved. Type material of this species is MFC-1P405.

6. *Conioscypha gracilis* (Munk) Zelski, Raja, A.N. Mill. & Shearer, Mycoscience 56 (3): 323 (2015)

≡*Debaryell agracilis* Munk, Botanisk Tidsskrift 51: 226 (1957)

≡*Cryptoleptosphaeria gracilis* (Munk) Rossman & Samuels, Stud. Mycol. 42: 185. 1999.

≡*Conioscyphascus gracilis* (Munk) Réblová & Seifert, Stud. Mycol. 50: 104. 2004.

Description and illustration: see Réblová & Seifert (2004)

Notes: *Conioscypha gracilis* was described by Réblová & Seifert (2004). This species has historically been reported in Argentina, Denmark, Japan from freshwater and terrestrial habitats on decayed wood (Minoura & Muroi 1978, Réblová & Seifert 2004)

7. *Conioscypha hoehnelii* P.M. Kirk, Transactions of the British Mycological Society 82 (1): 177 (1984)

Description and illustration: see Kirk (1984) and Chen & Tzean (2000)

Notes: Kirk (1984) described *Conioscypha hoehnelii* from bark of *Eucalyptus* sp., leaf of *Phormium tenax* J.R.Forst. & G.Forst. and an unidentified wood, all from U.K. Chen & Tzean (2000) reported it on a herbaceous stem in Huisun, Nantow Prefecture, Taiwan, China. See notes on *C. tenebrosa*. Type material of this species is IMI 249629a.

8. *Conioscypha japonica* Udagawa & Toyaz., Mycotaxon 18(1):132 (1983)

Description and illustration: Udagawa & Toyazaki (1983) and Chen & Tzean (2000)

Notes: *Conioscypha japonica* was isolated from scrapings and hair of male dog in Kobe, Japan. Later, this species was found by Chen & Tzean (2000) from a rotten herbaceous stem in Wulai, Taipei Prefecture, Taiwan, China. Although *C. japonica* has smooth conidia, the irregular pigments on the conidial wall makes the appearance rough, which is distinguishable from other *Conioscypha* species. Type material of this species is NHL 2915.

9. *Conioscypha lignicola* Höhn., Annales Mycologici 2 (1): 58 (1904)

Description and illustration: Shearer (1973), Chen & Tzean (2000)

Notes: *Conioscypha lignicola* is the type species of *Conioscypha* which was isolated from fallen wood of *Carpinus* on Mt. Gelber Berg, Weinerwald, Lower Austria. This taxon was also reported as a freshwater species on balsa wood at Laurel, Maryland, USA. Moreover, Chen & Tzean (2000) found *C. lignicola* on a rotten leaf of *Phyllostachys pubescens*, Huisun, Nantow Prefecture, Taiwan, China. *Conioscypha lignicola* resembles *C. boutwelliae*, *C. hoehnelii*, *C. japonica*, *C. minutispora*, *C. nakagirii* and *C. pleiomorpha* in having a central pore at base. However, the central pore of *C. lignicola* is surrounded by a dark brown ring. Type material of this species is IMI 270438.

10. *Conioscypha minutispora* Hern.-Restr., Gené & Guarro, Persoonia 32: 285 (2014)

Description and illustration: see Crous *et al.* (2014)

Notes: *Conioscypha minutispora* was saprobic on unidentified dead wood in Ucieda, Cantabria, Spain. See notes on *C. lignicola* and *C. pleiomorpha*. Type material of this species is CBS H-21464.

11. *Conioscypha nakagirii* Chuaseehar., Somrith., Suetrong & Boonyuen, Mycoscience 58 (6): 427 (2017)

Description and illustration: see Chuaseeharonnachai *et al.* (2017)

Notes: *Conioscypha nakagirii* was reported from decaying submerged wood in a stream in Pak Chong District, Nakhon Ratchasima Province, Thailand. *Conioscypha nakagirii* has distinguishable turbinate conidia which differs from other *Conioscypha* species. Type material of this species is BBH40587.

12. *Conioscypha peruviana* Zelski, Raja, A.N. Mill. & Shearer, Mycoscience 56 (3): 321 (2015)

Description and illustration: see Zelski *et al.* (2015)

Notes: *Conioscypha peruviana* was collected from submerged woody debris in Camanti, Cusco, Peru. This species was initially described from sexual morph. Conidia reproduced in culture are oblong, slightly curved that are similar with *C. fabiformis*, but *C. peruviana* contains lipid droplets in conidia. Type material of this species is ILL 41202.

13. *Conioscypha pleiomorpha* Hern.-Restr., R.F. Castañeda & Gené, *Studies in Mycology* 86: 85 (2017)

Description and illustration: see Hernández-Restrepo *et al.* (2017)

Notes: Hernández-Restrepo *et al.* (2017) introduced *C. pleiomorpha* from dead wood in Canary Islands, Spain. *Conioscypha pleiomorpha* has similar conidial morphology with *C. minutispora*, but conidia of *C. pleiomorpha* are larger than those of *C. minutispora* (13–18 × 12–14 vs 6–9 × 5–6 µm). Type material of this species is CBS H-21890.

14. *Conioscypha submersa* Z.L. Luo, K.D. Hyde & H.Y. Su, *Fungal Diversity* (2019)

Description and illustration: see Luo *et al.* (2019)

Notes: *Conioscypha submersa* was described on a decaying wood submerged in Nujiang river, Yunnan, China. See notes on *C. tenebrosa*. Type material of this species is MFLU 18–1639.

15. *Conioscypha taiwaniana* J.L. Chen & Tzean, *Botanical Bulletin of the Academia Sinica (Taipei)* 41 (4): 319 (2000)

Description and illustration: see Chen & Tzean (2000)

Notes: *Conioscypha taiwaniana* was introduced by Chen & Tzean (2000) from a decaying stem in Nantou Prefecture, Taiwan, China. Unlike some *Conioscypha* species that have conidia with central pore at the base, conidia of *C. taiwaniana* often taper towards a point at the apex. Moreover, *C. taiwaniana* develop the secondary conidia that are smaller in size than the primary conidia. Type material of this species is TNTU 1053.

16. *Conioscypha varia* Shearer, *Mycologia* 65 (1): 133 (1973)

≡ *Conioscyphascus varius* Réblová & Seifert, *Studies in Mycology* 50 (1): 101 (2004)

= *Cylicogone regenerans* Emden & Veenb.-Rijks, *Acta Bot. Neerl.* 22: 637 (1973)

Description and illustration: see Shearer (1973) and Réblová & Seifert (2004)

Notes: Shearer (1973) reported *C. varia* as saprobic from balsa wood, Patuxent River, Maryland, USA. Conidial morphology of *C. varia* are various. Type material of this species is ILLS 35119.

Discussion

The species of *Conioscypha* have a worldwide distribution and they are described from Africa, America, Asia and Europe (Chen & Tzean 2000; Zelski *et al.* 2015; Chuaseeharonnachai *et al.* 2017; Crous *et al.* 2018; Luo *et al.* 2019). Species in *Conioscypha* do not seem to have specific habitats preferences. Six species are reported from submerged wood in freshwater habitat, while eight species are saprobic on different hosts in terrestrial habitat, and two species was isolated from soil. However, *C. bambusicola* seems to have a specific host, and all *C. bambusicola* strains are reported from bamboo (Matsushima 1975, Chen & Tzean 2000). *Conioscypha japonica* is the only species that is found being parasitic in mammal (Udagawa & Toyazaki 1983), but this species can also be saprobic on rotten herbaceous stems (Chen & Tzean 2000).

The conidiogenesis in *Conioscypha* was well-studied by Shearer (1973) and Shearer & Motta (1973), and it appears to be intermediate between annellidic and phialidic. Single conidium is produced endogenously by percurrently proliferating conidiogenous cell (Shearer & Motta 1973). Goh & Hyde (1998) redescribed and broke down the process of conidiogenesis in *Conioscypha* into seven steps. At the same time, they introduced the *Conioscyphopsis* Goh & K. D. Hyde. Although *Conioscypha* and *Conioscyphopsis* share similar characters with micronematous conidiophores and aseptate, ovate or broadly ellipsoidal conidia, they have different conidial ontogeny and maturation. In *Conioscyphopsis*, conidiogenesis is enteroblastic-phialidic and single conidium is produced exogenously from determinate, but percurrently regenerating conidiogenous cells (Goh & Hyde 1998).

TABLE 3. A conidial morphological comparison in *Conioscypha*.

Species	Conidia			References
	Shape	Color	Size	
<i>C. aquatica</i>	Globose to subglobose	Dark brown to black	19–23 × 17–21 µm	Luo <i>et al.</i> (2019)
<i>C. bambusicola</i>	Ovoid or broadly obclavate, base truncate, apex apiculate	Dark brown	11–16 × 6–10 µm	Matsushima (1975)
<i>C. dimorpha</i>	Macroconidia: oblong to cylindrical, apex round, base truncate; Microconidia subglobose to oblong, apex round, base truncate	Macroconidia: olivaceous to brown; Microconidia pale brown	Macroconidia: 8–18 × 4–6.5 µm; Microconidia: 2.0–3.0 × 2.0–2.5 µm	Matsushima (1996)
<i>C. fabiformis</i>	Oblong or round, slightly curved	Olivaceous, black in mass	10–16 × 4.5–6.6 µm	Matsushima (1993)
<i>C. gracilis</i>	Ellipsoidal to flammiform, truncate at the base, slightly tapering towards apex	Reddish brown	8.5–9.5 × 5.5–7 µm, L/W 1.6:1	Zelski <i>et al.</i> (2015)
<i>C. hoehnelii</i>	Globose to subglobose or sometimes irregular, with a central pore in the inconspicuous scar at the base	Brown to dark brown	12–17 × 11–15 µm	Kirk (1984)
<i>C. japonica</i>	Obpyriform or subglobose, sometimes elongate, truncate at the base, broadly rounded at apex, smooth but with irregular pigments deposited at the periphery of the wall to give the appearance of roughness, with a pore at the point of attachment to the conidiogenous cell, entirely covered by a thin gelatinous sheath	Dark brown	9–14 × 4.5–10 µm	Udagawa & Toyazaki (1983)
<i>C. lignicola</i>	Obovate or sometimes subglobose, truncate at the base, with reduced lumina, smooth but dark dots deposited at the periphery, at the base with a central pore, surrounded by a dark brown ring	Brown	11–21.6 × 10.6–16.8 µm	Chen & Tzean (2000)
<i>C. minutispora</i>	Ellipsoidal, obovoid or subglobose, apex rounded, base truncate with a central pore	Dark brown	6–9 × 5–6 µm	Crous <i>et al.</i> (2014)
<i>C. nakagirii</i>	Turbiniate to pyriform, rounded at apex, truncate with a basal pore	Black	30–45 × 30–40 µm	Chuaseeharonnachai <i>et al.</i> (2017)
<i>C. peruviana</i>	Ellipsoidal to allantoid or fabiform, containing lipid droplets	Brown	13.5–18 × 5–8.5 µm	Zelski <i>et al.</i> (2015)
<i>C. pleiomorpha</i>	Ellipsoidal, obovoid or subglobose, base truncate with a central pore	Brown	13–18 × 12–14 µm	Hernández-Restrepo <i>et al.</i> (2017)
<i>C. submersa</i>	Globose to subglobose or ovoid	Pale brown, guttulate when young, dark brown to black when mature	17–19 × 15–17 µm	Luo <i>et al.</i> (2019)
<i>C. taiwaniana</i>	Ovoid or broadly obclavate, truncate at the base, often tapering towards a point at the apex	Olive brown to yellowish brown or dark brown	14.1–20.0 × 6.4–8.0 µm	Chen & Tzean (2000)
<i>C. varia</i>	ovoid, flammiform, naviculiform, or subellipsoid	Dark brown	8.4–15 × 5.6–8.5 µm	Shearer (1973)

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